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Summary

The range of Shovelnose Sturgeon (SVS) *Scaphirhynchus platorynchus* in the great rivers of central North America has contracted, but most remaining populations are considered stable, likely due to a combination of successful harvest regulations and longitudinal continuity of many river reaches, despite damming in upper reaches. The evolutionary relationships of SVS relative to sister taxa is still a matter of debate. Genetic diversity varies across the range, with substantial haplotype overlap among SVS and its congeners. Shovelnose Sturgeon mature early at 5–7 years, and spawn every 2–3 years. Some individuals may spawn in fall. Whether this species migrates is debatable, but individuals move long distances with larvae dispersing greater than 250 km, and adults moving >1900 km. Shovelnose Sturgeon appear to complete all aspects of their life cycle in the main channel of rivers, with sand and associated dunes playing an important role in station holding even at high flows. The greatest threats to this species include river temperatures exceeding 26°C that may impair growth and survival of young life stages, dams that impair movement during spring flooding, loss of critical mid-channel island habitats which may be important nursery areas, and increases in harvest pressure for the caviar trade. Given the broad distribution of this species across the jurisdiction of multiple states in the US, a species-wide conservation plan should be in place to ensure that SVS populations remain stable or increase.

Introduction

Sturgeon are among the most imperiled fishes in the world, with 27 species remaining on the planet. The Shovelnose Sturgeon (SVS), *Scaphirhynchus platorynchus* Rafinesque, 1820, also known as the sand sturgeon, the switchback, or the hackleback, is a benthic rheophilic species that is generally restricted to moderate to larger rivers throughout North America (Bailey and Cross, 1954). Unlike most sturgeon, they are not anadromous or catadromous, but complete their entire life cycle in rivers (i.e., potamodromous). Sturgeon are known for their long lifespan, high fecundity, and long time to maturation. This group may be considered to have one of the classic periodic fish histories (Winemiller and Rose, 1992), where they invest heavily in large, singular reproductive bouts that overlap with conditions conducive to survival of offspring. In this paper, we explore how SVS status and life history compares to those of other species, and speculate why this species seems to be persisting in much of its range while other sturgeon species are in peril. We review its evolutionary history, genetics, life history characteristics, and environmental/habit needs, predicting how SVS may respond to future threats.

Current distribution and status

Shovelnose Sturgeon are one of the most abundant and widely distributed sturgeon species in North America and perhaps the world, although they have been considered overfished and threatened in parts of their range (Colombo et al., 2007; Tripp et al., 2009; Hintz and Garvey, 2012). The species primarily resides throughout the Missouri, Mississippi, and Ohio river drainages, including several tributaries ranging in size from large order rivers to small creeks (Bailey and Cross, 1954). The current distribution has been reduced from what historical records indicate (Fig. 1). Range reductions have typically occurred in various upstream locations of tributary streams. For example, SVS currently reside in the Ohio River through the Ohio and Kentucky border, but previous records indicate occupancy up to Pennsylvania. Alterations to the upper Ohio River for navigation may have reduced habitat suitability for this species. Similarly, SVS inhabit the lower 200 km of the Platte River in Nebraska, but historically were found through the Platte River system into Wyoming. Documented extirpations have occurred in New Mexico (Pecos and Grande rivers), Alabama (Alabama-Mobile River basin), West Virginia, and Pennsylvania (Ohio River drainage). Several other states have reported local, but not complete, extirpations (Koch and Quist, 2010). Range reductions have likely occurred as a result of anthropogenic changes, mainly dam construction that inhabits population connectivity and reduces preferred habitat by converting river reaches to more lentic conditions.

The current distribution of SVS is continuous throughout the entire Missouri and Mississippi Rivers. This is contrary

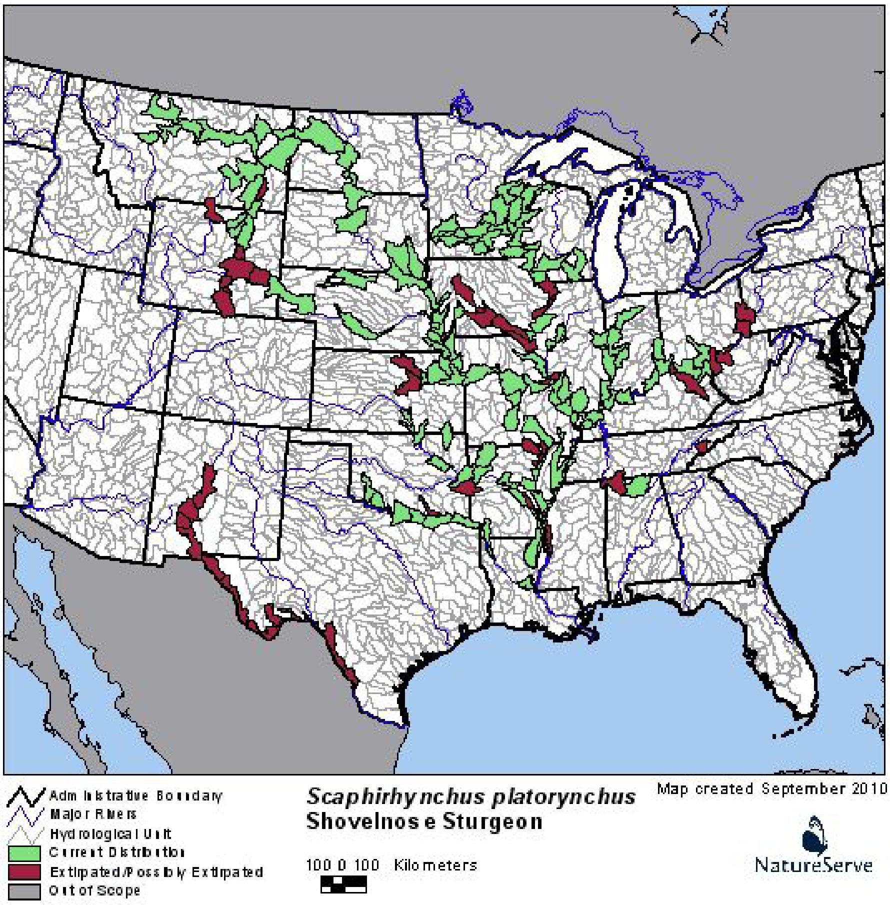

Fig. 1. Distribution of Shovelnose Sturgeon in the central US. From NatureServe.

to Pallid Sturgeon (PS) *S. albus*, a federally endangered congener in the US, whose distribution is fragmented throughout the Missouri and lower Mississippi River and completely absent from the Upper Mississippi River. We hypothesize that different life history characteristics likely allow SVS to inhabit smaller systems; thereby occupying and persisting through a much broader range. However, little research directly comparing the life history requirements of the two congeners has been done to answer why SVS are more resilient and abundant. In later sections, we will explore factors that allow SVS to persist in a changing environment.

The current literature suggests that SVS inhabit the following tributaries of the Missouri River: Yellowstone, Milk, and Tongue rivers in Montana; the Powder River in Wyoming; the Big Sioux and James rivers in South Dakota; the Niobrara, Elkhorn, and Platte rivers in Nebraska; the Kansas River in Kansas; and the Grand, Osage, and Gasconade rivers in Missouri. Within the Mississippi River, SVS reside in the Minnesota and St. Croix rivers in Minnesota; the Wisconsin River in Wisconsin; the Des Moines and Cedar rivers in Iowa; the Illinois and Ohio rivers in Illinois; the Wabash River in Indiana; the Arkansas River in Arkansas and Oklahoma; the White River in Arkansas; the St. Francis River in Arkansas and Missouri; the Red River in Louisiana, Arkansas, and Oklahoma; and the Atchafalaya River in Louisiana. This list is not intended to be exhaustive as SVS have been anecdotally reported in many other rivers and streams, particularly those that are continuously connected to rivers with known populations.

Very little information exists on the abundance of SVS. Historic qualitative information suggests that SVS were abundant throughout the Mississippi, Ohio, and Missouri Rivers. Previous accounts indicate that SVS were a nuisance to commercial fishermen because high densities saturated their nets (Coker, 1930; Barnickol and Starrett, 1951). High catch reports and proportion of catch in relation to other species suggest that SVS were a dominant component of the native riverine fish assemblage in these systems (Schmulbach et al., 1975; Moos, 1978). Fewer quantitative density estimates have been reported. Schmulbach (1974) estimated 2500 fish km^{-1} in the unchannelized Missouri River, and Helms (1973) estimated 1030 fish km^{-1} throughout the upper Mississippi River. Tributaries support comparatively fewer sturgeon, likely a result of the diminished size of lower order rivers, likely because of fewer resources or limited habitat. Estimated densities include 100 fish km^{-1} in the Red Cedar River in Wisconsin (Christenson, 1975), 500 fish km^{-1} in the Tongue River in Montana (Elser et al., 1977), and between 142 and 426 fish km^{-1} in the lower Platte River in Nebraska (Peters and Parham, 2008). Recently, Hintz et al., 2016 used mark recapture data to estimate the density of SVS in the 200-rkm Middle Mississippi River reach during 2002–2005, determining that there were 82 336 (95% CI = 59 438–114 585) adult SVS equating to 266 fish km^{-1}.

Many studies have reported trends in relative abundance. Different usage of sampling gears, sampling methodologies, and gear biases make abundance comparisons across management areas difficult. For example, SVS CPUE for electrofishing in the Wabash River, Indiana, averaged 24.3 fish h^{-1} and fluctuated from 4 fish h^{-1} to 478 fish h^{-1} (Kennedy et al., 2007), while Morrow et al. (1998) reported CPUE of 5.8 fish per 50-hook trotline. Doyle et al. (2008) examined variation in size structure and CPUE among multiple gears aimed at long-term monitoring of SVS. Mean CPUE varied from 0.3 to 9.5 fish, indicating that gear biases directly affect the ability to compare relative abundance across sampling gears.

Although the status of SVS populations has likely historically declined in the upper Missouri River basin (Keenlyne, 1997), populations have generally been reported as stable in recent years (Koch and Quist, 2010). According to state SVS biologists in the upper Missouri River basin most commonly cited habitat fragmentation due to dams, altered flow regimes, and declines in spawning habitat as the greatest threats to SVS populations (Koch and Quist, 2010). However, efforts are underway to directly and indirectly improve SVS populations and habitat. Specifically, fish passage efforts completed in 2012 at the Intake Diversion Dam in the Yellowstone River will prevent entrainment into the diversion canal and provide access to approximately 265 km of river (Koch and Quist, 2010). Additionally, reintroduction efforts in the Bighorn River in Wyoming have proved beneficial as reintroduced populations are experiencing increases in density and high somatic growth rates; although, natural SVS recruitment in the Bighorn River has not been documented since reintroduction (T. Annear, Wyoming Game and Fish, pers. comm.). In the upper Missouri River basin, SVS are only listed with a conservation status (i.e., species in need of conservation) in one state (i.e., Wyoming; Koch and Quist, 2010). There are no commercial SVS fisheries in the upper Missouri River basin whereas recreational fishing for SVS is allowed in Montana and Wyoming. Possession and harvest of SVS is illegal in North Dakota and South Dakota (Koch and Quist, 2010).

Upstream dams and channelization have greatly altered hydrology and physical habitat in the middle and lower Missouri River basins; however, populations have generally reported as stable since 1990 (Keenlyne, 1997; Koch and Quist, 2010). Main threats to SVS populations in the middle and Lower Missouri River basins include habitat fragmentation by dams, and loss of spawning and juvenile nursery habitats (Koch and Quist, 2010). Commercial harvest was considered a threat to the population in the lower Missouri River prior to 2010; however, federal listing of SVS as a threatened species under the similarity of appearance provision in the Endangered Species Act eliminated commercial harvest of SVS in the lower Missouri River and other areas where the two species (i.e., SVS and PS) are sympatric (United States Federal Register 75 FR 53598, September 1 2010). Prior to this listing, commercial harvest was allowed in the lower Missouri River downstream of Kansas City, MO but prohibited in the rest of the Missouri River. In addition to the federal listing in 2010, SVS are listed as a species in need of conservation in Iowa and Missouri (Koch and Quist, 2010). Regulated recreational fishing is permitted in the Missouri River and all tributaries in Nebraska, Iowa, Kansas, and Missouri.

The status of SVS populations in the upper Mississippi River basin is generally considered stable or unknown (Keenlyne, 1997; Koch and Quist, 2010). Commonly reported reasons for concern regarding SVS populations in the upper Mississippi River basin include reduced spawning habitat, habitat fragmentation, pollution, and roe harvest (Koch and Quist, 2010). Commercial harvest is permitted in the entire length of the Mississippi River in Wisconsin and Iowa; however, commercial harvest from the Mississippi River in Illinois and Missouri is only permitted upstream of the Mel Price Lock and Dam near Alton, IL. Regulated recreational fishing and harvest is allowed in all states in the upper Mississippi River basin; however, harvest is restricted in some tributaries (Koch and Quist, 2010). Shovelnose Sturgeon do not have any conservation status in Minnesota, Wisconsin, or Illinois (Koch and Quist, 2010).

In the middle and lower Mississippi River basin, SVS populations are considered stable in Missouri, Illinois, Arkansas, Oklahoma, and Mississippi (Koch and Quist, 2010). Louisiana reported increasing SVS populations since 1997, likely in response to the recent closure of the commercial fishery (Koch and Quist, 2010). Shovelnose Sturgeon are listed as threatened by the state of Texas and as a species in need of conservation in Arkansas, Oklahoma, Louisiana, and Mississippi. Common concerns regarding SVS persistence in the middle and lower Mississippi River basin included habitat fragmentation, changes to flow regimes, lack of spawning and juvenile nursery habitat, and commercial roe harvest (Koch and Quist, 2010). Currently, the only commercial SVS harvest in this basin is comprised of modest commercial fisheries in the White and Arkansas rivers in Arkansas.

The status of SVS populations in the Ohio River basin vary from unknown in Indiana, Ohio, and Kentucky to stable in Illinois. Shovelnose Sturgeon were considered extirpated in West Virginia and Pennsylvania; however, reintroduction efforts have been implemented in West Virginia (Koch and Quist, 2010). Additionally, SVS have been restocked into the Scioto River in Ohio. Although SVS have no conservation status in Kentucky and Illinois, they are listed as endangered in Ohio and a species in need of conservation in Indiana and West Virginia. Similar to other basins, the main concerns from biologists regarding SVS populations in the Ohio River basin are lack of spawning habitat, habitat fragmentation, and pollution (Koch and Quist, 2010).

In addition to the Mississippi River drainage, SVS populations were extirpated from the Rio Grande River and Pecos Rivers, and the Mobile-Alabama River basin (Keenlyne, 1997; Koch and Quist, 2010). Although extirpated in the state, SVS are listed as a species in need of conservation in Alabama. Effects from water development (i.e., dams) are cited as reasons for extirpation in New Mexico and Alabama (Koch and Quist, 2010).

Unlike its congener PS where recovery stocking is underway in the upper Missouri River, there have been few concerted attempts to supplementally stock or reintroduce SVS to reaches in which density is low. Because of its wide distribution, no standardized comparison of population density, presence/absence, or population viability has been conducted. A range-wide, standardized effort comparing population density and status (see Current distribution and status) is needed to assess the status of this species. In the following sections, we will specifically explore the evolutionary, life history, and habitat limitations that will affect conservation of SVS.

Evolutionary history and genetics

The SVS is included in the order Acipensiformes which is an ancient lineage that is believed to have existed for at least 200 million years (Bemis et al., 1997) within northern drainages of the supercontinent when North America and Asia were connected. The order Acipensiformes includes two families, Acipenseridae (sturgeon) and Polydontidae (paddlefish). Within Acipenseridae, four genera currently exist: *Acipenser*, *Huso*, *Scaphirhynchus*, and *Pseudoscaphirhynchus* (Birstein et al., 2002). The family Acipenseridae has been divided into two subfamilies: Acipenserinae which includes *Acipenser* and *Huso*, and the Scaphirhynchinae consisting of *Scaphirhynchus* (North American river sturgeon) and *Pseudoscaphirhynchus* (Asiatic river sturgeon; Birstein et al., 2002). The first North American SVS was described in 1820 by Rafinesque as *Acipenser platorynchus*, but in 1835 Heckel distinguished these river sturgeon from *Acipenser* due to the absence of spiracles (Forbes and Richardson, 1905). Because of this, the North American river sturgeon were given a new genus *Scaphirhynchus* (Forbes and Richardson, 1905). Despite fossils of ancestral *Scaphirhynchus* sturgeons dating from Late Cretaceous (Grande and Hilton, 2006), uncertainty in classification among the sturgeon species and phylogeny within the Acipensiformes, especially the Scaphirhynchinae still remains. There are two other extant species in the genus *Scaphirhynchus*: PS, *S. albus*, and Alabama Sturgeon (ALS), *S. suttkusi*.

All Acipenseriformes derive from a common ancestor that had approximately 120 chromosomes, twice the number of most Actinopterygian fishes. Paddlefishes share this complement as well, thus the initial genome duplication event, which was likely due to hybridization with the retention of genomes from both species (allopolyploidy), likely preceded the divergence of Polyodontidae and Acipenseridae in the Jurassic (Birstein and DeSalle, 1998; Fontana et al., 2008). One or more additional independent genome duplication events produced sturgeons with approximately 250 chromosomes, while allopolyploidy between sturgeons with approximately 120 and 250 chromosomes produced sturgeons with approximately 372 chromosomes (Fontana et al., 2008). Coincidentally the quantity of DNA per sturgeon cell varies in three classes of approximately 4.5, 9, and 13 pg DNA/cell (Blacklidge and Bidwell, 1993). Shovelnose Sturgeon have 112 chromosomes (Ohno et al., 1969) and approximately 4.7 pg DNA per cell (Blacklidge and Bidwell, 1993) and thus have the smallest and most ancestral genome size.

Several morphological and genetic studies have been conducted to determine how SVS fit into the tree of life given the uncertainty in identifying ancestral relationships within the subfamily Scaphirhynchinae. Many studies have used either osteological or morphological characters and found that the genera *Scaphirhynchus* and *Pseudoscaphirhynchus* are monophyletic or sister taxa (Bemis et al., 1997; Findeis, 1997; Dillman et al., 2007). Other studies using external morphology suggest that river sturgeons form a natural group, but *Pseudoscaphirhynchus* is paraphyletic and *Scaphirhynchus* is monophyletic (Mayden and Kuhajda, 1996; Kuhajda, 2002). Birstein et al. (2002) and Dillman et al. (2007) used molecular data to reject the idea of Scaphirhynchinae forming a monophyletic group. *Scaphirhynchus* may be basal to a clade containing all other living sturgeons (Krieger et al., 2008) and not closely related to *Pseudoscaphirhynchus* (Dillman et al., 2007). When Billard and Lecointre (2001) combined molecular and morphological data, they found the subfamily Scaphirhynchinae was monophyletic and the two genera within the subfamily were reciprocally monophyletic. Clearly, the phylogenetic relationships within the subfamily are not confidently resolved and likely will require more population-level genetic data across the taxa.

Within the genus *Scaphirhynchus* in what is now North America, Mayden and Kuhajda (1996) determined that SVS and ALS were morphologically more similar than either was to PS. Low levels of mtDNA variation and sharing of haplotypes between PS and SVS have thus far prohibited robust molecular phylogenies (Dillman et al., 2007; Krieger et al., 2008). So far, no fixed genetic differences between PS and SVS have been found using allozymes (Phelps and Allendorf, 1983), mitochondrial DNA (Campton et al., 2000), microsatellites (Tranah et al., 2001; Schrey et al., 2007), or single nucleotide polymorphisms (SNPs) (Eichelberger et al., 2014). However, each of these marker types, except allozymes, exhibit significant frequency differences among morphological species indicating some degree of reproductive isolation. While the number of specimens surveyed is small, all ALS surveyed to date exhibit a unique mtDNA haplotype that is very similar to common haplotypes in PS and SVS (Campton et al., 2000; Simons et al., 2001; Dillman et al., 2007). The low levels of variation among species of *Scaphirhynchus* is similar in magnitude to the level of divergence among intraspecific populations of many other fish species (Allendorf et al., 2001).

The sharing of alleles/haplotypes between SVS and PS, which are sympatric over much of their current ranges, may be due to a low mutation rate, recent (i.e., last few thousand years) common ancestry, and/or hybridization (Phelps and Allendorf, 1983; Campton et al., 2000; Tranah et al., 2004; Schrey et al., 2011; Eichelberger et al., 2014). Allozyme markers exhibited very low levels of polymorphisms with no alleles confined to either species and many loci difficult to interpret due to tetrasomic expression (Phelps and Allendorf, 1983). In a study of mtDNA (Campton et al., 2000), PS and SVS from the upper Missouri River basin were genetically distinct with PS exhibiting three haplotypes, one of which (haplotype 'A') was found in 17 of 19 fish surveyed. Haplotype 'A' was not found in upper Missouri River SVS, but it was common in Atchafalaya River SVS and absent in Atchafalaya River PS (Campton et al., 2000). Thus the mtDNA variation between

PS and SVS populations rivals that between PS and SVS at a single location. Studies of microsatellites (Tranah et al., 2001, 2004; Ray et al., 2007; Schrey et al., 2007) and SNPs (Eichelberger et al., 2014) also found frequency differences but not fixed differences between PS and SVS.

Shovelnose Sturgeon allele frequencies vary across their range. The most common mtDNA haplotype found in upper Missouri River SVS was absent from Atchafalaya River SVS (Campton et al., 2000). In a rangewide survey of microsatellite DNA variation, including samples from locations where PS do not occur, Schrey et al. (2009) found small but significant frequency differences among locations. A test for isolation by distance revealed a positive correlation between genetic and geographic distance (in river kilometers), but the trend was not significant (P = 0.055).

Shovelnose Sturgeon hybridize with PS in the wild (Carlson et al., 1985; Keenlyne et al., 1994; Tranah et al., 2001, 2004; Schrey et al., 2011) and PS are genetically (Allendorf et al., 2001) and morphologically (Murphy et al., 2007) more similar to SVS in the southern part of their shared range where hybridization is presumably more common (Schrey et al., 2011). Carlson et al. (1985) noted that while most *Scaphirhynchus* in the lower Missouri and Mississippi rivers were SVS, hybrids were as common as PS. Carlson et al. (1985) suggested that hybridization was recent and due to anthropogenic influences, and the study was cited as evidence that hybridization was a threat to PS when the species was listed under the United States Endangered Species Act in 1990 (United States Fish and Wildlife Service, 2010). In contrast, Allendorf et al. (2001) concluded that in the lower Mississippi, *Scaphirhynchus* was a hybrid swarm, and potentially a natural and ancient one, and that no pure PS remained there. Whether hybridization in *Scaphirhynchus* is natural or anthropogenic and how much of a threat it is to PS remains controversial. But is hybridization a threat to SVS? Generally, hybridization is seen as a threat to the rarer species as genes from the rare species become subsumed into the common one (Rhymer and Simberloff, 1996). As we will elaborate in a future section, Killgore et al. (2007) noted that in the Mississippi River the ratio of SVS to PS morphotypes decreased down river from 77:1 near the confluence with the Missouri River to 6:1 in the lower reaches, meaning that SVS are comparatively rarer in the south. Perhaps if *Scaphirhynchus* in the lower Mississippi River comprises a hybrid swarm and PS morphotypes are relatively common there, the genetic integrity of SVS is threatened there as well.

Morphology

Shovelnose Sturgeon is a member of the Chondrostei subclass and the Acipenseriformes order, they are primarily cartilaginous and lack a backbone with separate vertebrae, but instead have a notochord. Other characteristics of the family Acipenseridae are their elongated bodies covered in rows of scutes, barbels on the ventral surface of the rostrum, and the elongated upper lobe of the tail. Some characteristics specific to the genus *Scaphirhynchus* are lack of spiracles and a pseudobranchium (Bailey and Cross, 1954), a well-developed air bladder (Forbes and Richardson, 1920), an extremely flattened wide rostrum with fringed barbels and lip papillae (presumably to detect electric fields emitted by prey; Findeis, 1997 and Miller, 2004) and a long caudal filament with nerves and a lateral line along its length (Weisel, 1978). Sturgeon within the genus *Scaphirhynchus*, are known to be most benthic of the North American sturgeon (Warren and Burr, 2014). The wide but flat rostrum, large pectoral fins, flat ventral body surface, and bony scutes suggest that *Scaphirhynchus* sturgeon likely associate with the river bottom (Findeis, 1997; Hintz et al., 2016). It is also likely that *Scaphirhynchus* sturgeon compensate for poor swimming performance or relatively low swimming speeds with the ability to maintain position using the swift river currents without actively swimming using their large pectoral fins to generate negative lift (Adams et al., 1997, 2003; A. Porecca, unpubl. data).

Shovelnose Sturgeon are smaller in size (total length and head length) and darker in color than PS. Additionally, adult SVS have irregular rows of rhomboidal scutes covering the ventral side while PS tend to have a naked or smooth belly (Bailey and Cross, 1954), but often these general characteristics vary by geographic location and size (Kuhajda et al., 2007; Murphy et al., 2007). Because the PS and SVS are quite similar in appearance, many studies have been conducted to compare the morphology of these species resulting in the morphology of SVS well documented and the development of many morphological character indexes. When PS were first described by Forbes and Richardson in 1905, a group of characteristics were used to differentiate between PS and SVS. Some of the original characteristics were number of ribs (21–20 in PS and 10–11 in shovelnose), presence on SVS or absence of scutes on the belly of PS, and measurements of the head length (SVS have a shorter and wider head), and barbel placement (in SVS base of four barbels are in alignment, but in PS the outer barbels are behind the inner barbels). Since this time, other meristic and morphometric measurements have been compiled to develop characterization indices, used to identify adults in the field. Some common measurements taken to identify Ps, SVS or a hybrid sturgeon in the field are head length, interrostrum length (snout to outer barbel), mouth to inner barbel, length of inner and outer barbels, and mouth width (Bailey and Cross, 1954; Keelyne et al., 1994; Wills et al., 2002; Kuhajda et al., 2007; Murphy et al., 2007). Many researchers suggest that these indices should be used in conjunction with genetic markers to correctly assign species, especially when small specimens (300 mm) are being considered or hybrids could be present (Kuhajda et al., 2007; Murphy et al., 2007).

Reproduction

Shovelnose Sturgeon complete their entire life cycle within the rivers of North America, with both non-reproductive and spawning adults existing in these systems. Gametogenesis in SVS is similar to other sturgeon species and has been described by Colombo et al. (2007) and Wildhaber et al. (2007). Shovelnose Sturgeon in the middle Mississippi River (MMR) reach sexual maturity between 8 and 10 years for males and 9 and 11 years for females (Tripp et al., 2009), which is older than previously described by Keenlyne

(5 years for males and 7 years for females; 1997), revealing that there is considerable variation in maturation schedule within this species. Male SVS in the MMR become sexually mature at approximately 500-mm fork length, while females reached sexual maturity at approximately 570-mm fork length (Colombo et al., 2007). Spawning periodicity data suggests males spawn every 1–2 years, and females spawn every 3–4 years once sexual maturity is reached (Tripp et al., 2009), likely because it requires considerable energy to rebuild reproductive tissue. Mean fecundity of females was approximately 30 000 eggs (23.6 ± 1.26 eggs per gram of fish weight, Colombo et al. (2007); 21.7 ± 1.29 eggs per gram of fish weight, Tripp et al. (2009). Most SVS spawn in the spring (Colombo et al., 2007; Tripp et al., 2009). There is evidence of fall spawning as seen by ripe males and females with good quality gametes in September and October (Tripp et al., 2009), although larvae have not been found to date as a result of fall spawning. This however, may be an artefact of los sampling frequency for larvae during fall through winter. Whether there are temporally distinct spawning populations should be explored.

Both endogenous and environmental factors control the biological clock in sturgeon (see Webb and Doroshov, 2011). The relative importance of the environmental factors controlling reproduction and the magnitude of change of these factors required to initiate key gametogenic stages and a spawning event have not yet been well defined for many chondrostean species. In SVS, it is hypothesized that day length may likely initiate the post-vitellogenic phase defining a temporal spawning window, and within the spawning window, other short-term cues, such as water temperature, may modulate the spawning event (Papoulias et al., 2011).

The upper and lower lethal temperatures for SVS embryo survival were 8 and 28°C. This is based on newly fertilized embryos ability to survive, and optimal temperature for survival and development, it was predicted that SVS spawn in the wild from approximately 12–24°C, with mass spawning likely occurring from 16 to 20°C (Kappenman et al., 2013). Discharge does not appear to initiate spawning in SVS (DeLonay et al., 2009; Papoulias et al., 2011; Phelps et al., 2012; Richards et al., 2014), although extended periods of high discharge have been shown to lengthen the spawning season resulting in greater abundance of larval and age-0 SVS (Goodman et al., 2012). Given the importance of water temperature to spawning, thermal alterations have been identified as a concern to SVS (Phelps et al., 2010). Stratified reservoirs and hypolimnetic cold water releases from upper Missouri River dams may reduce SVS spawning habitat and inhibit or reduce embryo survival and development (see Development in early life).

Many sturgeon species are known to migrate from marine to freshwater ecosystems to spawn. SVS spawning migrations are restricted to the turbid, freshwater rivers of the US and are comparatively less well understood. Spawning SVS in the Missouri River above Fort Peck Dam moved both upstream and downstream during the spawning season seeking suitable spawning habitat (Richards et al., 2014). These results indicate that upstream migration is not a requirement for successful spawning as seen in the Missouri River below Gavins Point Dam (DeLonay et al., 2007, 2009). Surprisingly little is known about the presence or absence of annual migrations for spawning in this species given the large number of adult SVS implanted with transmitters in the Mississippi River. (see Habitat and ontogeny). Similarly, spawning habitat is presumed to be hard substrate in moderate flow (Bonnot et al. 2011). But few direct observations of actual spawning, egg distribution, and larval emergence have been made.

Development in early life

Presumably, fertilized eggs and developing embryos of SVS are dispersed over gravel and cobble in swift-flowing water and begin to drift after larvae emerge within 3–5 days, although attempts to capture these early stages in the Mississippi River failed many times (J. E. Garvey, unpubl. data). Field-based research with released larvae was successful (see Habitat and ontogeny). The sequence and timing of embryologic, larval, and juvenile development of SVS has been described from laboratory observations (Snyder, 2002; Colombo et al., 2007; Kappenman et al., 2013). In addition to SVS embryological stages (Colombo et al., 2007), larval length-specific morphological and diagnostic criteria are available for fish at least 10 mm in length (Snyder, 2002). Embryological and larval development of sturgeon species are similar and a staging system (Dettlaff et al., 1993) was applied to SVS (Colombo et al., 2007). Like other sturgeon species, embryo and larval development rate in SVS is temperature dependent (Shelton et al., 1997; Kappenman et al., 2013); the effect of temperature on SVS developmental rate fits an exponential relationship similar to other North American sturgeon species. At 20°C fertilized eggs hatch in 4 days; hatched yolk-sac larvae are ~7–9 mm; transition to exogenous feeding (also temperature dependent) occurs at ~8 days; and adult characteristics of fins and scutes are present at 26 days (Colombo et al., 2007). Preferences and thermal tolerances are greater for SVS than those reported for some North American sturgeon species and influence patterns of survival in the field (see Defining habitat). Early life stages of SVS are the most temperature sensitive. Newly fertilized embryos have a limited thermal tolerance ranging from approximately 12 to 24°C and an optimal temperature for survival and development near 17–20°C (Kappenman et al., 2013). Larval and juvenile SVS are capable of surviving for extended periods at a broad range of seasonally influenced temperatures. In laboratory studies, growth occurred at temperatures from approximately 12 to 30°C, the optimal temperature for growth was near 22°C, and the minimum temperature needed for growth was greater than 10°C (Kappenman et al., 2009). The reduction in weight observed in SVS held at <10°C suggests that extended periods of low temperature may deplete energy reserves and lead to higher mortality. While most SVS, when gradually acclimated to temperatures ranging from 26 to 30°C, were able to survive for an extended period (Kappenman et al., 2009), temperatures 26°C and greater can act as an environmental stressor leading to reduced growth rate and increased mortality (Kappenman et al., 2009; Phelps et al., 2010; Hupfeld et al., 2015). In controlled experiments with shorter acclimation periods, the lethal thermal maxima and point of loss of equilibrium of SVS were determined to range from ~30 to 35°C (Hupfeld et al., 2015; Deslauriers et al., 2016). Young of the year SVS thermal tolerance increased with greater body mass and acclimation temperature (Deslauriers et al., 2016). While upper thermal tolerances of SVS are similar to sympatric PS (Deslauriers et al., 2016), there appears to be differences in preference for thermal niches between SVS and PS (see Blevins, 2011; Meyer et al., 2011).

Habitat and ontogeny

Shovelnose Sturgeon, similar to other riverine fishes, rely on a mosaic of habitats in rivers throughout life to find appropriate locations for spawning, foraging, overwintering, and nurseries. These movements are complex and can include multiple steps that may require movement between and among rivers, potentially crossing multiple management jurisdictions, because states within the US are responsible for conserving species under most circumstances (Hintz and Garvey, 2012). Understanding the spatial extent of SVS movement across specific life-stages is fundamental to population management and conservation. This understanding is even more critical when the interactions between benthic riverine specialist (e.g., SVS) and anthropogenic river modifications are taken into account. Management of the Mississippi-Ohio-Missouri drainages for water is complex. A large extent of the three rivers and their tributaries maintain a navigational channel of 3 m, requiring a series of water training structures (e.g., dikes), dredging, and lock-dam complexes. The upper Missouri River differs in that it is dominated by a series of high-lift dams that permanently restrict the drainage of water flowing downstream. Factors influencing the movement and population dynamics of SVS may differ among river reaches or change as individuals move from one reach to another.

River fragmentation can disrupt natural drift patterns of larvae (Braaten et al., 2008), potentially disrupt spawning movement (Curtis et al., 1997), and reduce the foraging success of all life stages of SVS (Modde and Schmulbach, 1977). In laboratory studies, Kynard et al. (2002) found that SVS initiated downstream drift immediately after hatch and that the duration of larval drift was 4–5 days at low water velocities ($\leq$12 cm s^{-1}). Based on these findings, Kynard et al. (2002) estimated that the cumulative drift distance would be about 13 km. Braaten et al. (2008) moved this experiment to a side channel in the Missouri River and found that larval sturgeon were dispersed long distances downstream from the spawning and hatching locations. Their predictive cumulative drift model suggests that the average SVS would drift 95–250 km at water velocities between 0.3 and 0.6 m s^{-1}. If these finding were extrapolated to match the water velocities exhibited in the mainstem portions of the Missouri and Mississippi Rivers, the cumulative drift distances could be even longer and river fragmentation, such as that prevalent in the upper Missouri River, could have negative impacts on the availability of the length of free-flowing river needed to complete ontogenetic development (Braaten et al., 2008). This could also potentially mean that depending on spawning locations within each river, SVS spawned in the lower portion of the Missouri River could drift into the Mississippi River or SVS spawned in the Upper Mississippi River could drift into the Middle or Lower Mississippi River. Phelps et al. (2012) demonstrated that 30% of larval *Scaphirhynchus* sturgeon collected in the Middle Mississippi River originated from the Missouri, although the relative importance of these recruitment sources and the link between these natal and nursery habitats are still unknown.

In the past two decades, several studies regarding SVS yearly or seasonal movement among spawning, foraging, and overwintering habitats have been conducted in the Mississippi, Missouri, Yellowstone, and Kansas Rivers. Total or maximum movement varied among studies, depending on the river (impounded or obstructed versus free-flowing) with mean total movement ranging from 10.8 km (Hurley et al., 1987) and 18.5 km (Curtis et al., 1997) in the Upper Mississippi River to 53.6 km in the Yellowstone and Missouri Rivers (Bramblett and White, 2001). The highest total movement was recorded by Bramblett and White (2001) with SVS moving 254 km and up to 15 km day^{-1}. Recent telemetry studies combined with a network of stationary, data-logging receivers confirm past findings that SVS movement patterns are highly variable and that these fish are moving freely among connected rivers within the Mississippi River Basin (Goodman et al., 2012; S. Tripp, unpubl. data). S. Tripp (unpubl. data) found that SVS in the Mississippi River Basin on average move 180 km during the course of a year with a maximum movement observed at 1937 km.

The consensus among movement studies is that long range movements and the highest movement occurs in the spring which may be associated with spawning activities or seasonal shifts between overwintering and summer feeding areas; the lowest movement occurred in the winter (Hurley et al., 1987; Bramblett and White, 2001). SVS generally seem to show location fidelity during most seasons, but are capable of long-range movements when large reaches of unobstructed river are available (Hurley et al., 1987; Bramblett and White, 2001). As noted earlier, the reasons for movement such as spawning, dispersal, foraging are not well understood, although the prevalence of spring movement coinciding with spawning is a parsimonious explanation that needs more testing.

With advances in technology and numbers of transmitting-tagged SVS building, distance moved or potential migration paths by these riverine fish are becoming clearer and better understood. As population genetics suggest (see Evolutionary history and genetics), SVS populations are not isolated and mixing is common, meaning that SVS are crossing many geographical and political boundaries that encompass various state regulations. Therefore, in order to effectively manage or restore these highly migratory fish populations, inter-jurisdictional collaboration and basin wide considerations will be necessary.

Defining habitat

As mentioned earlier, movement and station holding of SVS has been well documented, but our understanding of its interaction with habitat is still in its infancy, largely because it is so difficult to sample these fishes in the field. Numerous factors have been implicated in negatively influencing SVS populations over the last 100 years (Keenlyne, 1997) with a particular emphasis placed on habitat degradation.

Habitats used by SVS can vary widely depending on the aquatic system, life stage, and diet (Phelps et al., 2010). Overall, a recent study by M. Hempel (unpubl. data) in the free flowing portion of the Mississippi River suggests marked differences in habitat use by life stage regardless of season. Adult SVS exhibit generalized habitat use, age-0 sturgeon exhibit specialized habitat use (specifically submerged sand bars with vegetation, Hintz et al., 2016), and juveniles exhibit intermediate tendencies relative to adult and age-0 conspecifics (Phelps et al., 2010). M. Hempel (unpublished) speculates that the habitats occupied by SVS may be related to macroinvertebrate consumption. Macroinvertebrates (i.e., Trichoptera, Diptera and Ephemeroptera) are likely abundant in habitats occupied by SVS and have been found to be the most important prey items in SVS diets in the Mississippi and Missouri Rivers (Carlson et al., 1985; Rapp et al., 2011; Seibert et al., 2011; Sechler et al., 2012, 2013). There has been speculation that side channel and backwaters are important for all life stages of SVS (likely relating to macroinvertebrate production), although these habitats appear to be used rarely (Gosch et al., 2015).

Adult SVS are generally thought to occupy locations associated with the main channel of rivers over sand, silt, or gravel substrates (Bailey and Cross, 1954; Hurley et al., 1987; Curtis et al., 1997; Gerrity et al., 2008; Phelps et al., 2010). Adult SVS in the pooled portion of the Upper Mississippi River occupied the riverine section at varying depths (e.g., 1–10 m), velocities (0.05–0.65 m s^{-1}), and sand or rock substrate (Hurley et al., 1987). In a follow up study also in the Upper Mississippi River, adult SVS were located most often in tailwater habitats, sand substrate, relatively low velocity (0.23 m s^{-1}) and moderate depths (5.8 m) (Curtis et al., 1997). In the Missouri River above Fort Peck Reservoir in Montana, SVS utilized shallow depths (2.31–2.48 m), sand, silt, and rock substrate coupled with a narrower range of velocities (0.48–0.55 m s^{-1}) among seasons (Gerrity et al., 2008). SVS in the Missouri and Yellowstone rivers were located in sand and gravel substrates at a broad range of depths and velocities (Bramblett and White, 2001). Quist et al. (1999) found SVS in the Kansas River in shallow depths (1–2 m), wide-ranging velocities (0.02–0.79 m s^{-1}), and sand substrate. Sand dunes appear to be an important habitat for SVS as well (Hintz et al., 2016).

Despite the relative importance of understanding habitat needs during early life history, minimal information for age-0 SVS exists (but see Phelps et al., 2010). Pre-settlement movement (i.e., drift) can be extensive (Braaten et al., 2008; Phelps et al., 2012) and drift occurs within 0.5 m of the bottom (Braaten et al., 2008). Post-settlement habitat varies. In the Missouri River, age-0 SVS were most frequently captured in swift water (0.5–0.7 m s^{-1}) with channel sandbars, rootless-dikes, and wing-dikes and were rarely found at L-dikes, along banklines, or in tributaries where bottom velocity was slower ($\leq$0.2 m s^{-1}). Hintz et al. (2016) found that young SVS prefer featureless sand and sand dune areas relative to gravel and vegetated areas in experimental areas.

Thermal alterations have been identified as a concern to the growth and survival of SVS (Phelps et al., 2010). Stratified reservoirs and hypolimnetic cold water releases from upper Missouri River dams may reduce SVS spawning habitat, inhibit or reduce embryo survival and development, and decrease productivity and forage habitat in affected downstream reaches (Everett et al., 2003; Kappenman et al., 2009, 2013). Excessively warm temperatures have been described to cause direct mortality to SVS and negatively affect population level dynamics (Phelps et al., 2010; Hupfeld et al., 2015; see Defining habitat). While water temperature rarely exceeds 30°C in most of the range, thermal threats that exceed tolerances have been identified (high summer river temperatures, loss of riparian habitat, power plant thermal effluent, etc.), and climate change concerns raised (Hupfeld et al., 2015; Deslauriers et al., 2016). We speculate that climate warming may cause the range of SVS to contract northward as southern regions become too warm for growth.

Population status and dynamics

Although many management agencies report populations as stable (see Current distribution and status), surprisingly little is known about the population trajectory of SVS throughout its range. This is largely because of gaps in knowledge about vital rates such as natural and fishing mortality, relationships between adult density and recruitment, and reliable patterns of age and maturation. Observed differences in size structure and growth are apparent throughout the range of SVS, which are likely due to patterns of harvest and perhaps other factors affecting mortality and density. Tripp et al. (2009) found that mortality was increasing and recruitment declining for SVS in the Mississippi River where harvest was occurring. In an assessment of growth throughout the distribution of SVS, Hamel et al. (2015) found that SVS grew quickly and attained maturity faster in areas that were heavily influenced by commercial fishing harvest or river modification (i.e., middle Mississippi and lower Missouri Rivers) and grew slowly and delayed maturity in areas of less anthropogenic influence (i.e., upper Mississippi and Wabash Rivers). However, SVS populations that had larger maximum sizes and ultimately, greater longevity generally displayed slower growth. Thus, patterns of harvest suggest that density-dependence is important in sturgeon and that compensatory responses are likely important. One of the most important factors influencing population estimates involves reliable aging. Age information has been attained from age assignments from sectioned pectoral fin rays. Despite the widespread use of fin rays for estimating age, recent research has indicated substantial variability in both the accuracy and precision of fin ray generated age estimates (Whiteman et al., 2004; Hamel et al., 2014; Rugg et al., 2014).

Other threats

The rivers of the US are subject to other negative impacts such as direct effects of barge navigation, altered water quality, and degraded substrates. Barge traffic on the Mississippi and Ohio Rivers is high, with most tows including 15 barges, with propellers that can extend to the river bottom and potentially contact benthic sturgeon. Miranda and Killgore (2013) conducted a study in the Upper Mississippi River where they quantified the number of SVS entrained by propeller wash of a tow boat. They found that the number of SVS entrained annually was 0.38 sturgeon ha^{-1}, which combined with other sources of mortality may reduce population growth. Regulations mandated by the Clean Water Act are relatively recent, and the rivers of the Central US continue to receive effluent from sewage treatment plants, non-point pollution from agriculture and urban runoff, and other factors such as high sedimentation. Legacy contaminants such as polychlorinated biphenyls (PCBs) continue to accumulate in the tissues of SVS which can influence sex determination and reproductive output found that, The occurrence of female gametes in male gonads (intersex), was present in up to 15% of male SVS and positively related to PCB concentrations, especially those in brain tissue (Koch et al. 2006). Exposure to these contaminants during early life interfered with sexual differentiation and may affect male spawning success (Koch et al. 2006). Rivers such as the Illinois River that are dammed and receive high levels of agricultural runoff are experiencing a marked increase in sedimentation. The loss of coarse and sand substrate in this river and other tributaries could greatly inhibit the ability for SVS to complete their life histories.

Prognosis

The SVS is a unique species among fishes and among sturgeon, especially in that the species seems to be relatively stable in much of its historic range despite habitat modification, harvest, damming, hydrograph alteration, pollution, navigation, and other environmental effects. Perhaps because of this status, no range-wide management and conservation plan exists. This is problematic because rapid response to future threats will be impossible without a comprehensive, knowledge-based tool at the disposal of managers.

There is much conjecture about why this species is faring better than other sturgeon, including the endangered PS which occurs in sympatrically throughout much of its range. Likely foremost is that much of the rivers within the range of SVS are managed for navigation rather than flood control, meaning that gates are open during high flow when telemetry studies showed that this species has moved most frequently. The small size and early maturation of SVS likely allow them to respond more quickly to perturbations in the environment by increasing reproductive output through earlier maturation and perhaps more frequent spawning. The jury on fall spawning remains out, but if true, fall spawning may afford additional flexibility to responding to environmental variability. Unlike PS which become piscivorous during adulthood, SVS remain foraging generalists, relying on insect prey that are likely more resilient to environmental modifications than prey fish.

The phylogenetic relationships and genetic diversity of SVS remain largely unresolved. This species is clearly derived from an ancient lineage, but its relationship with other living relatives remains unclear. Genetic divergence, especially with PS, appears to be very recent geologically, and hybridization may be threat in locations where SVS are rare relative to PS. Maintaining genetic diversity throughout the range of the species is going to require more information about existing differentiation in haplotypes, especially in reaches where SVS are rare or isolated.

Insufficient information exists today to assess the range-wide threats to SVS (but see Bajer and Wildhaber, 2007 for an assessment in the lower Missouri River). Inter-basin connectivity, differences in management (e.g., harvest allowed or prohibited), habitat availability, passage opportunities, and many other factors need to be incorporated into predictive models. Focusing on dynamics in individual river reaches, especially when both larval exchange and adult movement occurs among them, is going to yield limited management guidance.

Research needs

To create a range-wide conservation plan, information gaps need to be identified and answered. Genetics combined with movement data will refine our understanding of the diversity among SVS and how to maintain genetic integrity. The extent of movement, especially migrations of adults and dispersal of young, is not well understood, although many promising techniques and experimental approaches have greatly extended our current knowledge. Bottlenecks to population growth such as recruitment, adult survival, and the influence of external factors such as harvest, pollutants, and altered river morphology and hydrology need to identified. Range wide monitoring stratified across reaches of various sizes needs to be standardized to assess the trajectory of populations through time.

Probably one of the greatest threats to the persistence of SVS is the unpredictable effects of climate change. Increased variability in precipitation may influence patterns of discharge, which may interfere with spawning. More likely, increases in temperature may make southern portions of the range uninhabitable for young and perhaps adult SVS. Thermal refuges within river channels will be necessary. Given the popularity of caviar and its high price, pressure to re-open many SVS fisheries to harvest will continue in the future. If this happens, managers must have the proper monitoring and assessment tools available as well as appropriate population benchmarks to ensure sound management of this resource.

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